AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3190, 30 pp., 16 figures, 1 table March 3, 1997

The Bird Flies, Genus *Carnus*: Species Revision, Generic Relationships, and a Fossil *Meoneura* in Amber (Diptera: Carnidae)

DAVID GRIMALDI[1]

ABSTRACT

Variation in the male genitalia of *Carnus* and other features reveal that specimens from eastern and northern North America are the same as the European species, *C. hemapterus* Nitzsch, 1818. A *Carnus* from western North America is newly described, *C. occidentalis,* n.sp., as are two new species from Florida (*C. floridensis*, n.sp.) and central Mexico (*C. mexicana,* n.sp.). Specimens of two probable additional species from southern Mexico are also discussed, for which only female specimens are available. Single records of the genus from southeast Asia and Africa indicate that the genus is probably global, but yet uncovered in most areas because of the specialized collecting required to find them. All host records of *Carnus* are summarized and new ones presented. The flies are exclusively nest associates of birds, the adults probably being hematophagous parasites of the nestlings. Larvae of *Carnus* are described for the first time. They are most distinctive for the single, midventral row of eight fleshy protuberances.

A new species of carnid is described in 20 million-year-old (Miocene) amber from the Dominican Republic, *Meoneura vieja,* n.sp., belonging to the sister genus of *Carnus.* This is the first carnid known from the Caribbean. The only other fossil carnid is in Eocene Baltic amber. Ages of the two fossil species are consistent with their phylogenetic rank, and suggest that carnids probably originated in the Paleocene, when many other families of "acalyptrate" Cyclorrhaphan flies were also radiating.

INTRODUCTION

In the nests of various birds, primarily in the Holarctic Region, a curious tiny fly sheds its wings: *Carnus.* Europeans have been studying *Carnus hemapterus* Nitzsch since

[1] Curator and Chairman, Department of Entomology, American Museum of Natural History.

ISSN 0003-0082 / Price $3.60

ary LeCroy, Dept. of Ornithology AMNH) kindly checked and updated the xonomic names and classification of the list bird hosts. Development of the museum's nber collection is made possible by the enerosity of Chairman Emeritus of the mu- um, Robert G. Goelet. My field and labo- tory research on Dominican amber has een sponsored by NSF grant BSR 9020102. Pinned material was received on loan from e following institutions and their respective rators:

M	Australian Museum, Sydney (D.K. McAlpine)
AS	California Academy of Sciences (P.H. Arnaud, Jr.)
NCI	Canadian National Collection of Insects, Ottawa (J. Cumming)
NHM	Hungarian Natural History Museum (L. Papp)
UMB	Zoologische Institut, Humboldt Museum, Berlin (H. Schumann)
HS	Illinois Natural History Survey (Kathleen Methven)
HNP	Musée d'Histoire Naturelle, Paris (L. Tsacas)
HRS	Naturhistoriska Riksmuseet, Stockholm (B. Viklund)
MNH	U.S. National Museum of Natural History, Smithsonian Institution (W. Mathis)
TSU	Utah State University (W. Hanson)

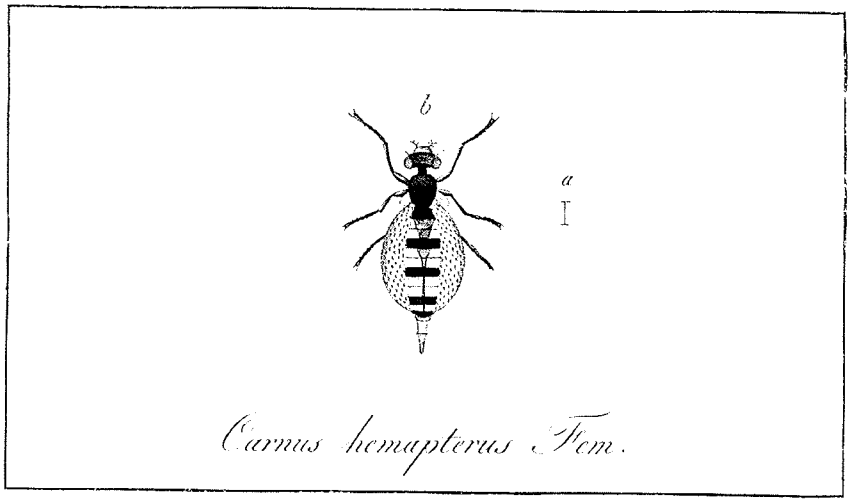
SYSTEMATICS

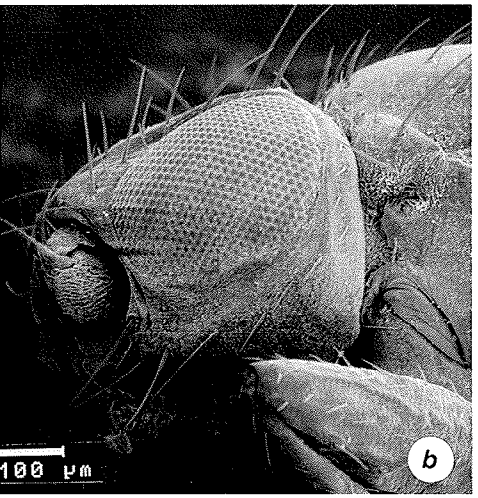
GENUS *CARNUS* NITZSCH

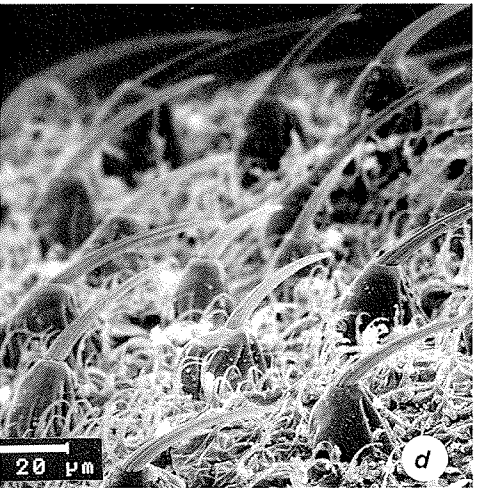
YPE SPECIES: *Carnus hemapterus* Nitzsch, 1818.

arnus Nitzsch, 1818: 305; Collin, 1911 (synonymy of *Cenchridobia*).
enchridobia Schiner, 1862: 435.

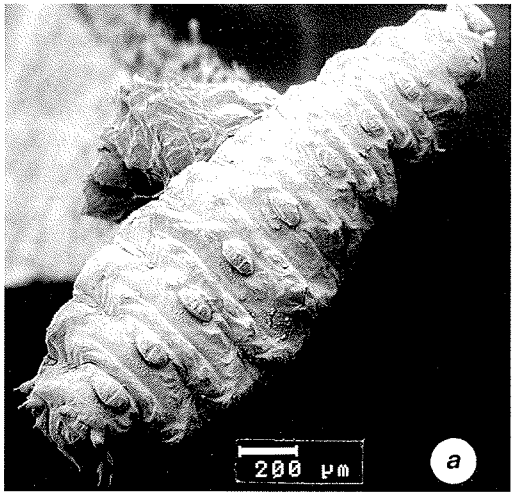
DIAGNOSIS: Tiny flies living primarily in

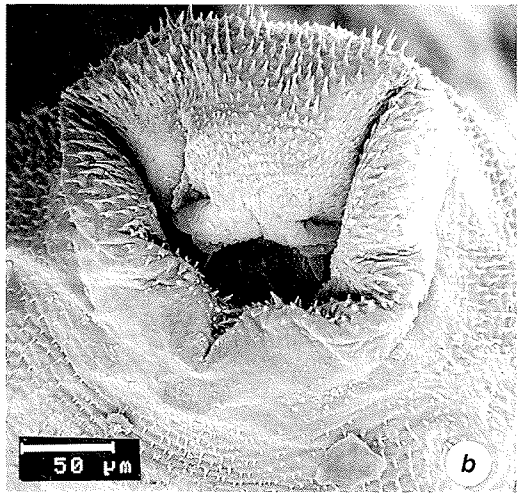


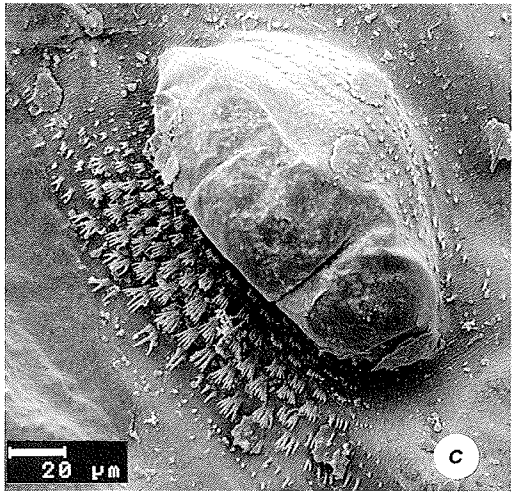


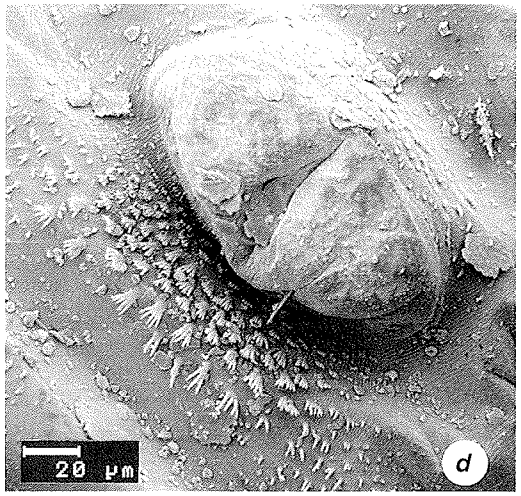


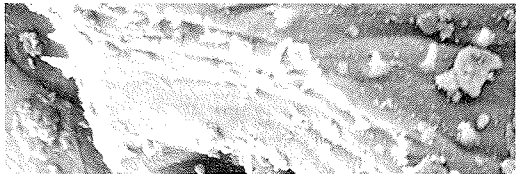
electronmicrographs of *C. occidentalis,* n.sp. **a.** ofile. **c.** Base of dehisced wing, which is broken nterior crossvein. **d.** Setulae in the abdominal, d, conical base.





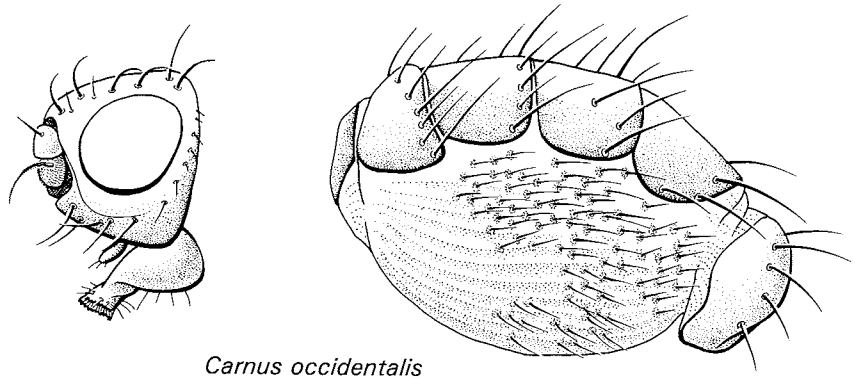




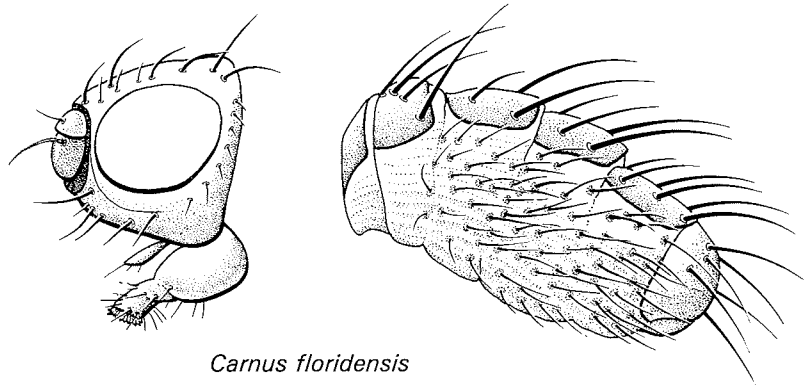


böl, Kelt VIII//13/70, Papp, 1♂; Alcsüt, I/20/63, Csókofésze K böl Kelt, Warga, 3♂ iss. no. 18); Szentendre, III-V/70, Papp, ♂ (diss. no. 17). **Sweden:** Sk. Malmö. Bel-viegården, Kläckt ur holk nr. *Sturnus vul-aris,* 28/IV/86, 10♂ (diss. nos. 19, 20), 4♀ NRS). **Switzerland** (all in HNHM): Kauf-orf, Sur poussin de Cherèche, 3/VI/79, Bau-e, 1♂ (diss. no. 16), 2♀; Anière (GE), nest *Falco tinnunculus,* 9/VI/79, Baude, 3♂. **USA: Colorado:** Colorado Springs, I/18/70, R.M. Stabler, ex: Sparrow Hawk, ♂ (diss. no. 7), 2♀ (NMNH); **Indiana:** *Wayne Co.,* Centerville, 5/VIII/61, G.L. Ward, *Sturnus vulgarus* nestling, 1♂ (diss. o. 4) (NMNH). **Maryland:** *Howard Co.,* VI/85, ex: young kestrels in nest box; Low-e, Martin, and Wallace, 2♂ (diss. nos. 1,), 2♀ (NMNH). **Massachusetts:** *Middle-x Co.,* Cambridge, 7/VII/81, N.E. Woodley, ♂ (diss. no. 12) (NMNH). **New Jersey:** *ape May Co.,* Avalon, VI/5/79, W.G. Rob-haud, ex: osprey nestling, 1♂ (diss. no. 2), ♀ (NMNH). **New York:** Albany, IV/4/72, A. Wilcox, 2♂ (NMNH); *Tompkins Co.,* haca, ex: falcon (no date or coll.), 1♂, 1♀ NHS); Jamesville, J.R. Philips, VI/24/76, : nest of American kestrel, 2♂ (CNC). **hode Island:** Richmond, VI/1/71, A. Lav-lee, 3♂ (diss. nos. 3, 10), 3♀ (NMNH). **tah:** *Cache Co.,* Smithfield, 27/V/74, T.L. Whitworth, magpie nest in willow, 7♂ (diss. o. 21), 8♀ (UTSU, 1 of each sex in MNH); West Nibley Lumber Mill, 16-18/ /74, T.L. Whitworth, magpie nest, Nos. 758, 1788, 3♂ (diss. no. 22), 2♀ (UTSU).

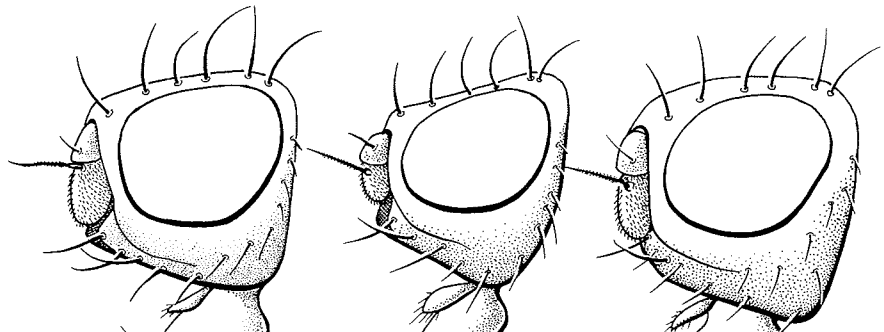
HOSTS: Bequaert (1942) summarized the osts and localities for European specimens d records of *Carnus hemapterus,* which in-uded 29 species of birds in 15 families. He

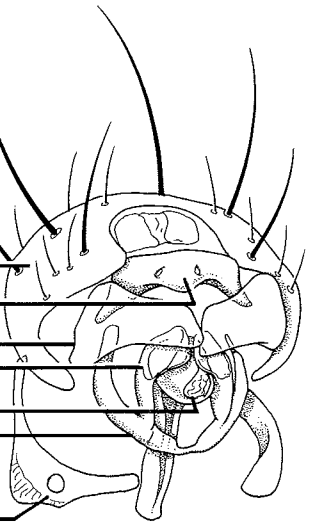


Carnus occidentalis

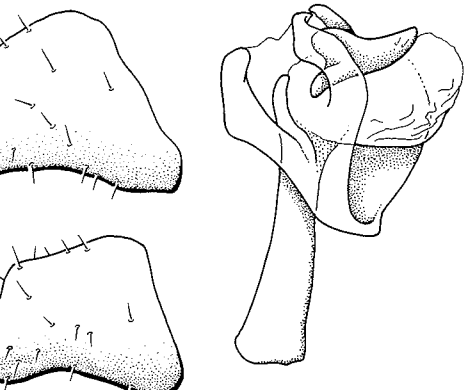


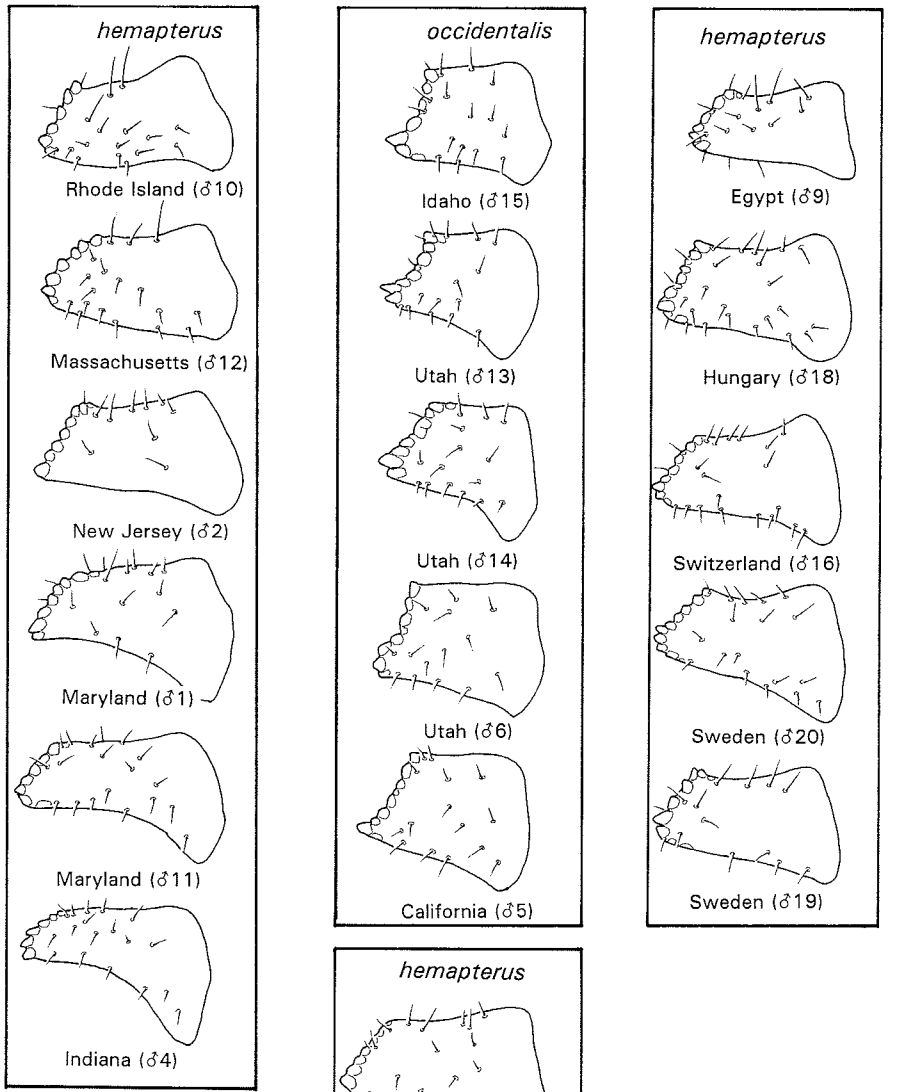
Carnus floridensis





C. hemapterus
(Egypt, ♂8)





alic region is entirely covered with simple nbranched) spinules (fig. 3b). The posterior d has five pairs of lobes (fig. 3e), and the sterior spiracles are retractable enough to entirely recessed (fig. 3f).

DISTRIBUTION: European records of *Carnus mapterus* were summarized by Bequaert 942), which included the following coun-es: Austria, Finland, Germany, Italy, Lith-nia, the Netherlands, Romania, Switzer-nd, and Yugoslavia. Additional records are ain (Carles-Tolra [1993]), Hungary (Papp, 84; this study), eastern Russia (Papp, 84), and Sweden (Papp, 1984; this study). pp (1984) also listed "Nearctic and Afro-pical Regions" under the distribution of *hemapterus*; some of these records, as own below, refer to other species.

American records of *Carnus* were most re-ntly reviewed by Capelle and Whitworth 973), with new records cited by Fitzner d Woodley (1983) and Cannings (1986). ates and provinces previously reported are: izona (Bequaert, 1951: species identity un-rtain, specimens were possibly *occidental-* n.sp.), Baja California (Bequaert, 1951; brosky, 1965: probably *occidentalis,* sp.), British Columbia (Bequaert, 1951; annings, 1986), Florida (Bequaert, 1942: obably *C. floridensis,* n.sp., see below), In-ana (Wilson, 1977), Massachusetts (Main d Wallis, 1974), New Brunswick (Sabros-, 1965), New Jersey (Kirkpatrick and Col-n, 1989), New York (Bequaert, 1942), Utah loyd and Philip, 1966; Capelle and Whit-orth, 1973: included *hemapterus* and *occi-ntalis,* but these species were not distin-ished at the time), Washington state (Fitz-r and Woodley, 1983, specimens of which uld have been *occidentalis* or *hemapterus*).

sonal commun.) (orientation of the mount prevents a definitive identification, but the male specimen appears to be *hemapterus*). Previous authors maintained that this might represent a disjunction of eastern and western populations. *Carnus hemapterus* clearly occupies the eastern half of North America, and northern latitudes west to northern Utah and southern British Columbia (fig. 9). *Carnus occidentalis,* n.sp., is the fly former authors called *hemapterus* from southwestern North America.

An apparent absence of *Carnus* in midwestern North America may be attributable to the poor sampling for these flies, but the distinct identity of the western North American species (reported below) suggests the disjunction to be real. Indeed, an examination of bird nests from western Montana revealed no *Carnus* (Jellison and Philip, 1933). Prior to the present study, virtually no comparisons had been made among individuals of *Carnus* from various localities. Bequaert (1942) mentioned that he was unable to compare European and American specimens, but did note (on the basis of old descriptions) that the setation in the abdominal pleural membrane was slightly different in the American specimens, and the "[external] male terminalia [were] virtually identical." Given that apparent Holarctic species are often two species, Nearctic and Palearctic (albeit subtly different), separate identities are not surprising.

Carnus orientalis

Carnus orientalis Maa, 1968: 33.

DIAGNOSIS: Separated from *hemapterus* and *occidentalis* by *orientalis* having a narMalaysia ("Selangor, Rantau Panjang, 8 km N. Klang, ex: juvenile fish owl"). Holotype is in the Bishop Museum, Honolulu (no. 7604), paratypes in the Natural History Museum, London; and the National Museum of Natural History, Smithsonian Institution.

It should be noted that an intensive survey of nearly 70 bird nests, from 23 species and eight families of birds, done in Hokkaido, northern Japan, revealed no *Carnus* (Iwasa et al., 1995).

Carnus occidentalis, new species

Figures 2, 3, 6, 7

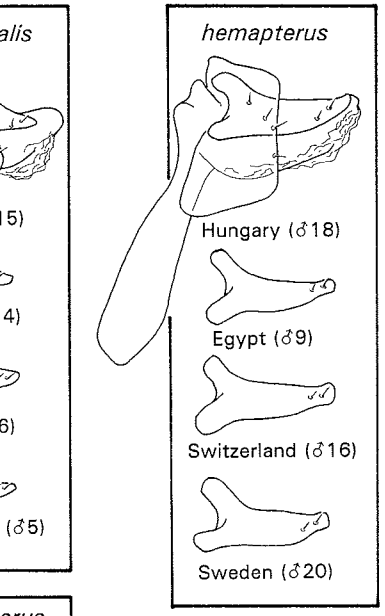
DIAGNOSIS: Very similar to *C. hemapterus* but consistently distinguished from it by male genitalia in *occidentalis* having a shorter, deeper surstylus that is almost square (apical width/total length approximately 0.57, vs. 0.30 to 0.45 in *hemapterus* [fig. 6]); paraphysis (paramere) in lateral view much shorter, almost triangular (greatest width/greatest length = 0.75, vs. 0.55 in *hemapterus*) (fig. 7).

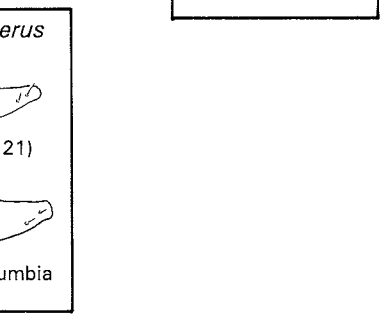
Head, notum, pleura light, shiny brown to black; proclinate interfrontal setae cruciate; ocellar setae almost parallel; antenna with pedicel tan, flagellomere 1 dusty gray. Notum with apical scutellar setae cruciate, leg coloration typical for genus. Setulae on abdominal pleural membrane short, longer ones dorsad. Male genitalia: synsternite VII + VIII, a vestigial pair of crescentic sclerites flanking epandrium; paraphysis (paramere) longer than wide; surstylus with blunt teeth on medial edge, trapezoidal in shape, longer than wide.

TYPES: Holotype (male): UTAH: *Box Elder Co.,* Mantua, Devil's Gate, ex: flicker

PALEARCTIC

ERN





yses and other parts of the male genitalia in *C.*

(head, all of thorax, labium, femora, most of each tibia). Antenna with pedicel and flagellomere I dark, black-brown. Ocellar setae divergent; proclinate interfrontal setae convergent but not cruciate; labium bulbous. Setulae on pleural membrane of abdomen black, about twice the length of setulae in other species. Female tergites narrow, except tIV (W/L = 2.2 [vs. 2.4–3.6 in other species]); tergites with long setae on posterior margin, about twice the length of setae in other species. Male genitalia with epandrium having long, stout setae, about twice the length of other species; synsternite VII + VIII complete dorsally; aedeagal apodeme short (ca. 0.7× length in other species); paraphysis a simple, triangular shape; surstylus rectangular, not trapezoidal, with blunt teeth on the apical edge.

TYPES: Holotype (male): FLORIDA: *Wakulla Co.,* 15/V/92, on woodpecker nestling (diss. no. 24). Paratype: female, same data. Both specimens in AMNH.

ETYMOLOGY: In reference to the type and only known locality, in Florida, USA.

Carnus mexicana, new species

Figures 4e, 5d–e, 8b

DIAGNOSIS: Coloration light brown to tan, all tarsi yellowish white. Head: Proclinate interfrontal setae convergent, but not cruciate; ocellar setae parallel to slightly divergent; vibrissae with large distance between two ipsilateral ones (distance approx. 5× the diameter of the seta). Thorax: scutellar setae with apical pair parallel to convergent (in very replete females they are cruciate from pressure of the abdomen). Abdomen: pleural setae short; female tergites narrower than in

ETYMOLOGY: In reference to Mexico, the only known locality.

Carnus sp. A

Figures 4c; 8c

FEATURES: Larger black species; ocellar setae divergent; proclinate interfrontal setae upright, almost parallel, another pair posteriad and nearly cruciate. Proboscis slightly longer and thinner than in other species (except *Carnus* sp. B), labellum small and narrow. Abdominal setae (pleural setulae and tergal setae) black, long. Male unknown.

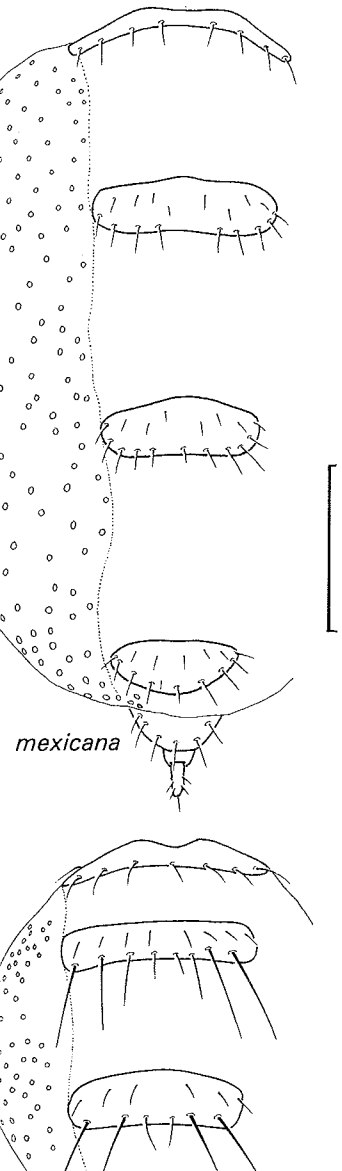
SPECIMENS: **MEXICO:** *Chiapas,* 8 mi E. San Cristobal, 19/V/69, B. Peterson, ex: owl nest. 2♀. In CNC.

DISCUSSION: Both this species and *Carnus* sp. B appear to be distinct species on the basis of somatic features only. However, since the other species of *Carnus* in this study are most consistently diagnosed on the basis of male genitalia, I hesitate to describe these as new species without additional material. *Carnus* sp. A and B are sympatric at least in southern Mexico, but were reared from different hosts.

Carnus sp. B

Figure 4d

FEATURES: Body entirely dark, black-brown, except for eyes and light yellowish tarsi. Proboscis slightly longer and thinner than in other species (except *Carnus* sp. A), labellum narrow. Proclinate interfrontal setae virtually upright, convergent to almost parallel. Eye longer than high, cheek very deep; vertex flat in profile. Apical scutellar setae with tips virtually touching. Tergites not observed well, since specimens considerably



kingfisher, *Halcyon albiventris*. Since this kingfisher is widespread through South Africa, Gabon, Zaire, Kenya, and Somalia, the fly is thought to be similarly widespread. If this *Carnus* is as polyphagous as the European and North American species, it probably feeds on many birds. A description of this species will be published by DeConinck.

GENERAL DISCUSSION

All but one of the more than 65 records of *Carnus* associate the fly with nests of tree-nesting birds (appendix 1) (the one exception is the mention by Maa [1968] of *Carnus hemapterus* on the gray egret, *Ardea cinerea,* in The Netherlands). More than one-third of the records report *Carnus* in raptor nests, 10 records in woodpecker nests, 9 with corvids, and the remaining records being one to four reports each in various families of smaller, perching birds (passeriformes). The apparent predilection for raptors may be due to the conspicuous size of the nests, and the carrion debris that falls into the bottom of the nest, in which larval carnids would breed. Later I discuss why tree-nesting birds are parasitized.

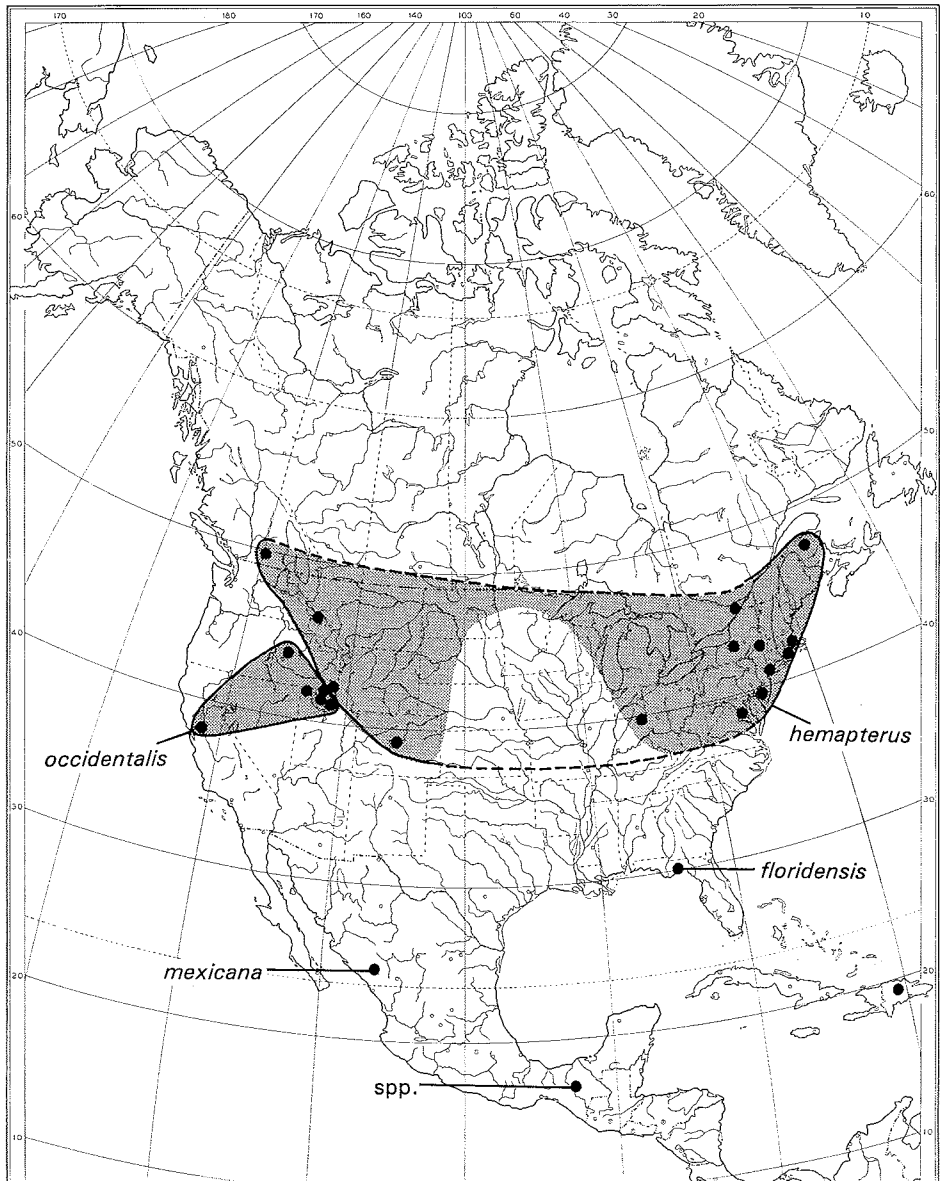
Behavior of the flies and field observations indicate that the flies specifically feed on blood and/or oily and other secretions of nestling birds. This is probably their sole way of life, given the distinct adaptations of *Carnus* for avian ectoparasitism, such as dehiscent wings; short, stiff setae over much of the body; and physogastry. Presumably, an enormous clutch of eggs or one or more large larvae are produced with the volume of blood/oil meal that distends the female abdomen two to three times the size of the rest

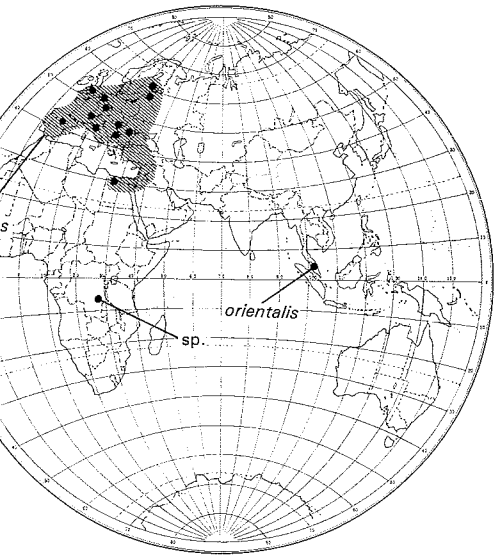
ism rates of birds may be high, the flies have little noticeable effect on the birds. *Carnus hemapterus* was found on 91 of 103 (88%) nestling barn owls (*Tyto alba*) in southwestern New Jersey (Kirkpatrick and Colvin, 1989). The flies were on the chicks only until the fifth week. In Germany, *Carnus hemapterus* infested nestlings of the starling, *Sturnus vulgaris,* from hatching, and the heaviest infestation was when the nestlings were six and seven days old (Walter and Hudde, 1987). Parasitism apparently did not reduce breeding success of the starlings.

Adults of *Carnus* probably do not disperse with their avian hosts. No reports have ever been made of banded, mist-netted, wild-captured or even domestic birds having *Carnus* on them. The flies may just be much easier to detect in a nest or nest hole and on nestlings and fledglings. However, *Carnus* lacks modifications seen in fleas and other ectoparasitic Diptera (such as hippoboscids, streblids, and nycteribiids), which allow the parasite to grip the hairs or feathers of its flying or moving host. These include an extremely flattened body (for moving among hair and feathers) and combs (ctenidia) or strong claws for gripping. *Carnus* also lacks the distinctive ectoparasite feature of reduced eyes. If *Carnus* must disperse to nests simply by its own flight, instead of by phoresy, then the broad range of hosts seen in *C. hemapterus* must be directly related to this method of host colonization.

Three of the five species of *Carnus* are each known from only a single series or pair of specimens from one nest (e.g., *orientalis, mexicanus, floridensis*). This applies as well to three additional, undescribed species from Mexico and Africa. No records exist from

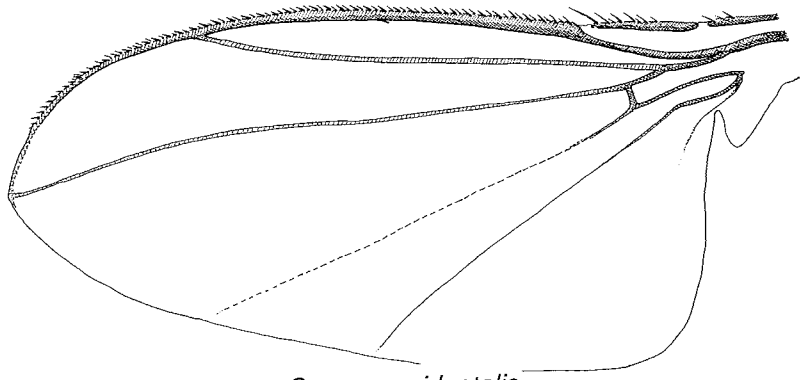
ngth of flagellomere I. Vibrissae stout, sub-
nded by 4 pr. of subvibrissal setae: pair im-
ediately ventral to vibrissae smallest, next
ir similar in size and orientation to vibris-
e; setae of large lateral pair upturned and
vergent; lateralmost pair convergent. Pro-
oscis with small palps and labellum; pre-
entum only slightly bulbous, considerably
naller than in *Carnus*. Face width/head
idth = 0.41; cheek depth/eye depth = 0.34.
Thorax: Notum with flat dorsal surface;
rostichal setulae well developed, not in
ws. Setae: 1 large postpronotal; 1 presu-
ral (lateral); 2 notopleurals (anterior one
ightly stouter); 1 pr. large prescutellar ac-
stichals; 2 supra-alars; only 1 (large) pair
dorsocentrals; 2 pr. scutellars. No color
atterns distinct on thorax or abdomen.
ings: completely hyaline. Section of costal
ein proximal to sc break with row of 5
out, black, spinelike setae (no indication of
line of weakness in this area). R_{2+3} short.
ostal vein ending midway between apices
R_{2+3} and R_{4+5}. Crossveins dm-cu and r-m
esent, separated by a distance approxi-
ately 1.5 times length of crossveins. Vein
$_1$ very light, barely noticeable. Vein A_1
rgely absent. Wing length = mm. *Legs*:
orefemur with dorsal row of 3 and ventral
w of 4 long setae; midtibia with 2 large
ical setae; hind femur with ventral row of
-6 stiff short setae on distal half, one seta
ice the size of others.
Abdomen: Male and female tergites 2–4
rtually devoid of setae, with only 2–3 setae
ear lateral margins. Tergite 5 with normal
tation, including row of larger setae along
osterior margin. Tergite 6 minute, with sev-
al long setae, segment 7 with 2 lateral
ates. Pleural membrane of segments 1 and



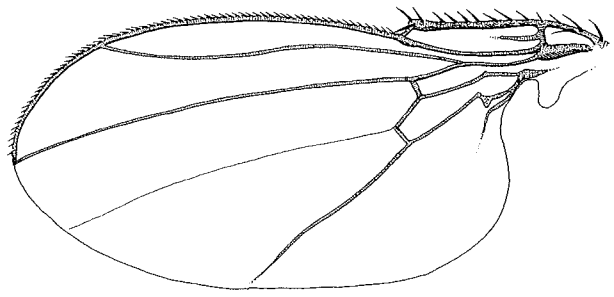


and records of *Carnus*.

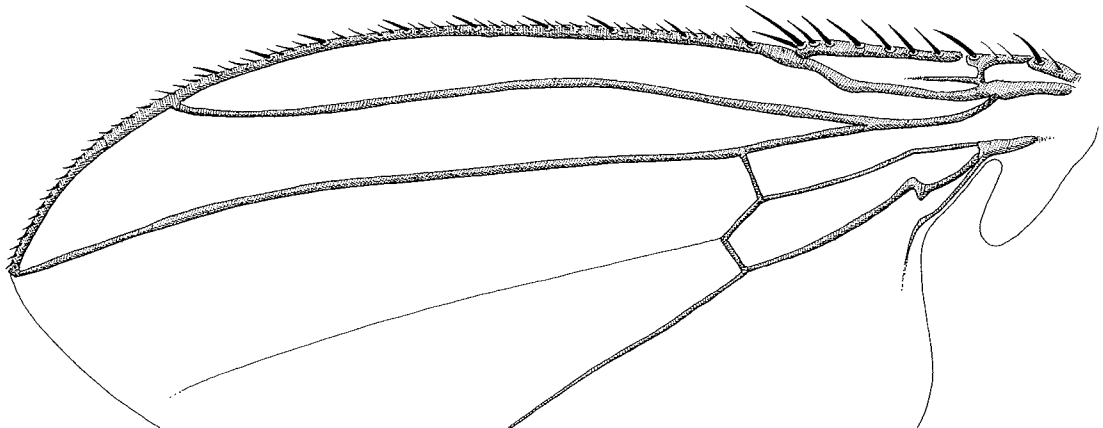
2. Apomorphic: One pair of dorsocentral setae present. Plesiomorphic: Two pairs.
3. Apomorphic: Pair of (proclinate) inner frontal setae present. Plesiomorphic: None present.
4. Apomorphic: Aedeagus (phallus) long, coiled, with extensive spicules. Plesiomorphic: short, bare.
5. Apomorphic: Female cerci fused (McAlpine, 1989). Plesiomorphic: Cerci not fused.
6. Apomorphic: Bases of antennae (pedicel, flagellomere I) recessed into deep fossae. Plesiomorphic: Fossae not present.
7. Apomorphic: Facial carina broad, at least width of antenna. Plesiomorphic:

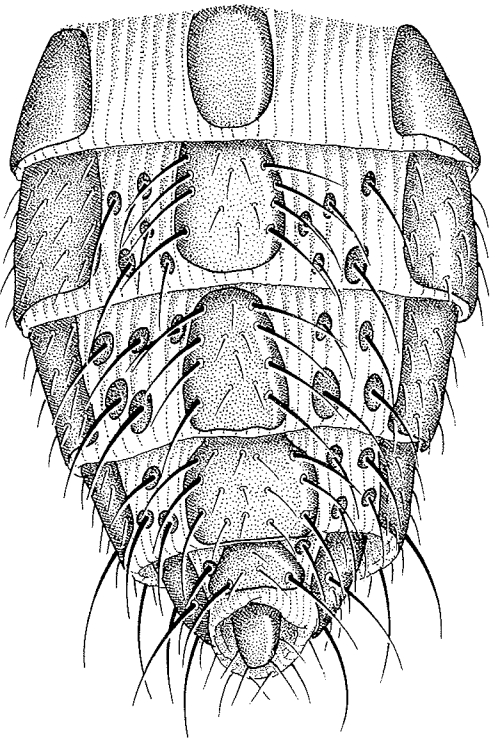


Carnus occidentalis

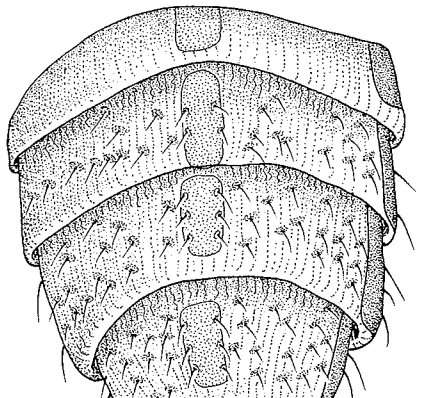


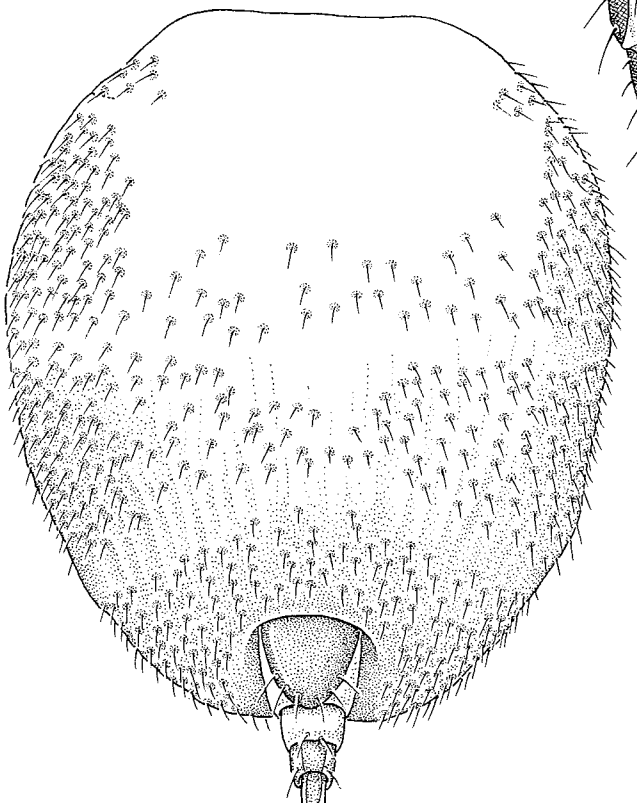
Meoneura vieja

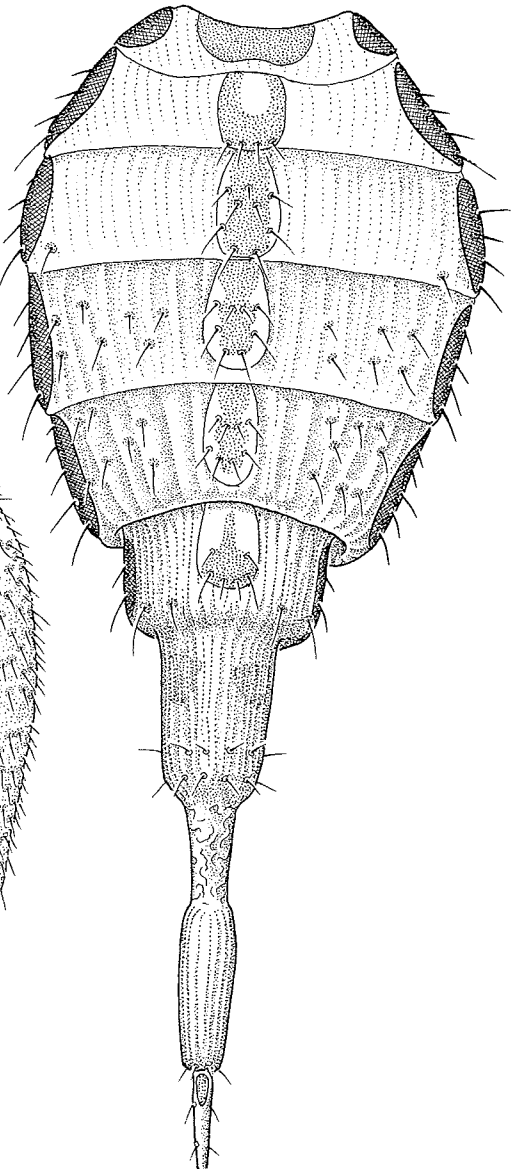


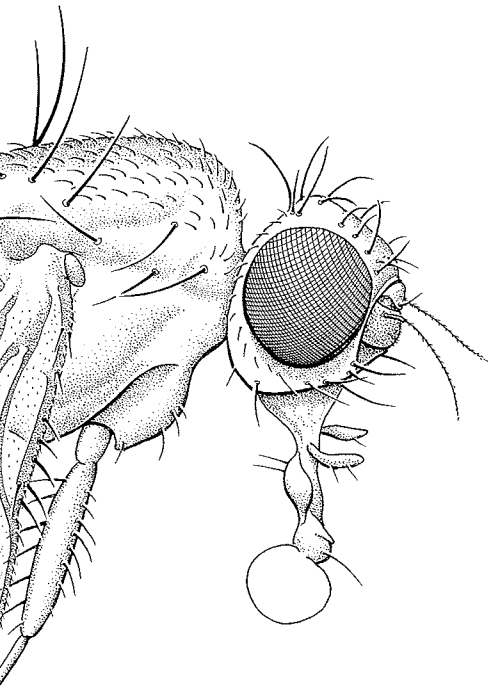


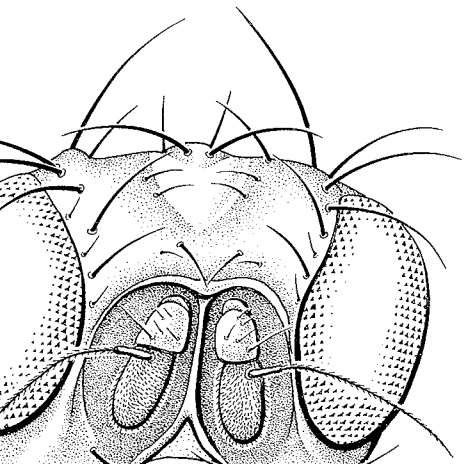
Meoneura digitata

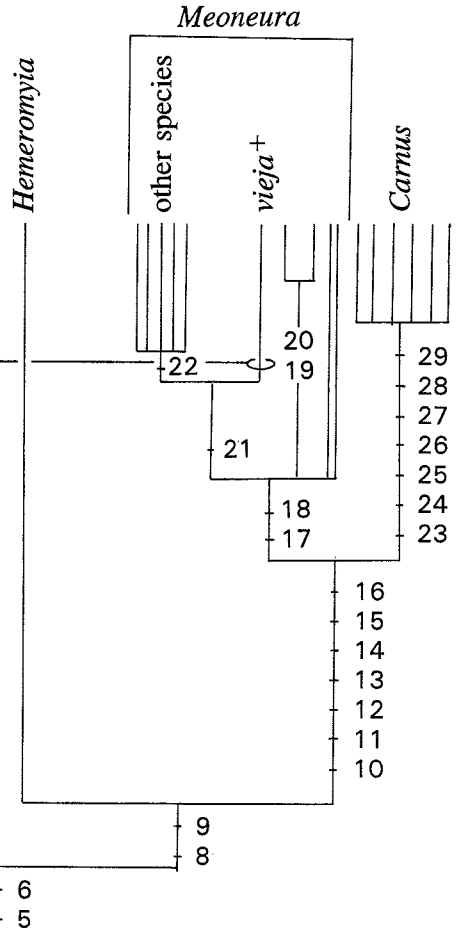












Carnidae. No attempt was made here to define

many undescribed species from New Zealand and Australia, where they breed in beach wrack. The clade of *Neomeoneurites* (two species in Chile [Hennig, 1972; Wheeler, 1994]) and the Baltic amber fossil, *Meoneurites* Hennig (1965), is defined on the basis of a broad facial carina (character 7). Wheeler (1994) discussed several apomorphic male genitalic features of living *Neomeoneurites,* the existence of which are unknown for the fossil *Meoneurites.* It is interesting that, without the Baltic amber fossil, one would have assumed that the early history of the carnids was entirely an austral one (as based on *Australimyza* and *Neomeoneurites*). The extinction of present-day austral taxa from northern latitudes has actually been discussed elsewhere, specifically with respect to organisms in Baltic amber (Ander, 1942). The next taxon on the cladogram is *Hemeromyia,* a genus of four Palearctic, two Nearctic, and one African species. Little is known of its biology, but the report by Cole (1969), of specimens in New Mexico reared from the nest of a mouse (*Peromyscus truei*), is consistent with what is known of the habits of other carnids.

The close relationship between *Meoneura* and *Carnus* has never been questioned and rests on substantial morphological criteria: characters 10–15, above. It is possible, in fact, that *Carnus* may eventually be found to be paraphyletic with respect to *Meoneura,* since only two characters of *Meoneura* are known thus far to be apomorphic with respect to *Carnus*: the spinose base of the costal vein in *Meoneura* (character 17), and the close proximity of the crossveins on the wing of *Meoneura* (character 18) (which is impossible to evaluate for *Carnus,* since the distal

Male genitalia of *Meoneura* offer a plethora of features for cladistic analysis of the genus. However, for purposes here only certain obvious features were selected to group some species. One feature, character 20, groups the North American species *Meoneura pteropleuralis* Sabrosky and *M. digitata* Sabrosky (fig. 12, top). At least four North American species (*californica, lamellata, flavifacies,* and *wirthi*) and one European species (*milleri* Gregor) are grouped on the basis of characters 21 and 22. The fossil *Meoneura* appears to be a basal member of this clade, since it possesses character 21 but not 22. One should not expect this preliminary attempt at cladistics of *Meoneura* to necessarily make much biogeographic sense, particularly in light of the very poor Neotropical sampling of this genus. However, it can be assumed on the basis of these relationships that the genus *Meoneura* possibly originated in the lower Miocene to late Oligocene.

With an Oligo-Miocene origin of *Meoneura,* and appearance of the more plesiomorphic clade, *Meoneurites* + *Neomeoneurites,* by the time of the Eocene Baltic amber, the Carnidae can be assumed to appear by the Paleocene. Given the virtual lack of higher cyclorrhaphan fossils from the Cretaceous, carnid origins in the Paleocene would be entirely consistent with radiations of the modern families of Cyclorrhapha in the earliest Tertiary.

EVOLUTION OF HOST USE: Like most carnids, *Meoneura* is closely associated with feces of mammals and birds. In fact, there are several records of *Meoneura* in close association with birds. *Meoneura lamellata* was reported about the "openings of sand mar-

erous ectoparasites, the preening and ruffling of stiff, adult contour feathers would probably prevent the adult flies from reaching the skin. Whatever the mode of host evolution, the parasitic lifestyle of *Carnus* adults is derived from behavioral and morphological specializations that further used the contents of the nest: its inhabitants.

The *Meoneura* in amber were preserved almost certainly when flying around trunks of the amber tree (*Hymenaea*). It is plausible that they were breeding in or searching for the nests of birds in *Hymenaea* trees, since feathers are also preserved in Dominican amber. One feather, in fact, has been identified as from a woodpecker (family Picidae), probably closely related to the extant Antillean Piculet (*Nesoctites micromegas*) (Laybourne et al. 1994).

CES

idae) in North America. J. Med. Entomol. 10: 525–526.

Carles-Tolra, M.
1993. A new species of *Geomyza,* with new acalyptrate records to the Iberian peninsula (Diptera, Acalyptrata). Hist. Anim. 2: 49–55.

Cole, F. R.
1969. The Flies of Western North America. Berkeley: Univ. California Press.

Colless, D., and D. K. McAlpine
1991. Diptera. *In* The insects of Australia. Melbourne Univ. Press.

Collin, J. E.
1911. On *Carnus hemapterus* Nitzsch (*Cenchridobia eggeri* Schiner) and its systematic position among the Diptera. Novit. Zool. 18: 138–139.
1930. Some species of the genus *Meoneura*

Nitszch. Schriftenr. Phys.-Oek. Ges. Königsberg 53: 1–18.

Dobroscky, I. D.
1925. External parasites of birds and the fauna of birds' nest. Biol. Bull. 48: 274–281.

Engel, E. O.
1919. Dipteren, die nicht Pupiparen sind, als Vogelparasiten. Z. Wiss. Insektenbiol. 15: 249–258.

Fitzner, R. E., and N. E. Woodley
1983. *Carnus hemapterus* Nitzsch from Swainson's hawk. Raptor Res. 17: 28–29.

Germar, E. F.
1822. Fauna Insectorum Europae. Fasc. IX, pls. XXIV–XXV.

Griffiths, G. C. D.
1972. The phylogenetic classification of Diptera Cyclorrhapha, with special reference to the structure of the male postabdomen. The Hague: Junk.

Grimaldi, D. A.
1987. Phylogenetics and taxonomy of *Zygothrica* (Diptera: Drosophilidae). Bull. Am. Mus. Nat. Hist. 186: 103–286.
1993. The care and study of fossiliferous amber. Curator 36: 31–49.
1995. The age of Dominican amber. *In* K. B. Anderson and J. C. Crelling (eds.), Amber, resinite, and fossil resins. Am. Chem. Soc. Symp. Ser. 617: 203–217.

Guigan, C., H. Launay, and J. Beaucournu
1983. Ectoparasites des oiseaux en Bretagne. 1. Répartition et écologie d'un diptère hématophage nouveau pour la France: *Carnus hemapterus* Nitzsch [Cyclorrhapha, Carnidae]. Revue Fr. Entomol. 5: 54–62.

Hennig, W.
1937. Milichiidae et Carnidae. *In* E. Lindner (ed.), Die Fliegen der palaearktischen Region 60a: 91 pp. Stuttgart: E. Schweizaerbart'sche Verlagsbuchhandlung.

pan (Diptera). Can. Entomol. 127: 613–621.

Jellison, W. L., and C. B. Philip
1933. Faunae of nests of the magpie and crow in western Montana. Can. Entomol. 65: 26–31.

Kirkpatrick, C. E., and B. A. Colvin
1989. The ectoparasitic fly *Carnus hemapterus* (Diptera: Carnidae) in a nesting population of common barn owls (Strigiformes, Tytonidae). J. Med. Entomol. 26: 109–112.

Laybourne, R. C., D. W. Deedrick, and F. M. Hueber
1994. Feather in amber is earliest New World fossil of Picidae. Wilson Bull. 106: 18–25.

Lee, R. D., and R. E. Rychman
1954. Coleoptera and Diptera reared from owl nests. Bull. Brooklyn Entomol. Soc. 44: 23–24.

Lloyd, G. D., and C. B. Philip
1966. The "wingless" fly, *Carnus hemapterus* Nitsch [sic] (Milichiidae), on hawk fledglings in northern Utah. J. Parasitol. 52: 414.

Maa, T. C.
1968. A new *Carnus* from Malaysia. Pac. Insects 10: 33–36.

Main, A. J., and R. C. Wallis
1974. Primary records of two vertebrate ectoparasites in New England (Acarina: Argasidae and Diptera: Milichiidae). Proc. Entomol. Soc. Washington 76: 427.

McAlpine, J. F.
1989. Phylogeny and classification of the Muscomorpha. *In* J. F. McAlpine and D. M. Wood (eds.), Manual of Nearctic Diptera 3: 1397–1518. Agric. Canada Monogr. 32.

Mercier, L.
1928. Contribution à l'ètude de la perte de la

1987. Carnidae. *In* J. F. McAlpine (ed.), Manual of Nearctic Diptera 2: 909–912. Agric. Canada Monogr. 28.

Schiner, J. R.

1862. Vorläufiger Commentar zum dipterologischen Theile der "Fauna austriaca." V. Wien Entomol. Monschr. 6: 428–436.

Stobbe, R.

1913. Zur kenntnis der Gattung *Carnus* Nitzsch (= Cenchridobia Schiner) mit 1 nov. sp. (Dipt.). Dtsch. Entomol. Z. 1913: 192–194.

Valter, G., and H. Hudde

1987. *Carnus hemapterus* (Milichiidae, Diptera), an ectoparasite of nestlings. J. Ornithol. 128: 251–255.

Wheeler, T. A.

1994. A new species of *Neomeoneurites* (Diptera: Carnidae) from Argentina, with a discussion of male postabdominal structure in the genus. Can. Entomol. 126: 435–441.

Wilson, N. S Bull

1977. Ectoparasites found in the nest cavities of pileated woodpeckers in Oregon. Bird-Banding 48: 171–173.

APPENDIX

Bird Host Family/Species	Location	Nest (N)/ Bird (B)	Carnus Species	Ref.
ARDEIDAE:				
Ardea cinerea	Netherlands	B	hemap	f
PANDIONIDAE:				
Pandion haliaetus	New Jersey	B	hemap	i
ACCIPITRIIDAE:				
Haliaetus albicilla	Finland	N	hemap	a
Aquila heliaca	Yugoslavia	B	hemap	a
Buteo swainsoni	Washington	B	h/occ	b
Buteo jamaicensis calurus	Utah	B	h/occ	c
FALCONIDAE:				
Falco peregrinus	California	B	occid	i
	Finland	N	hemap	a
	Germany	B	hemap	k
Falco tinnunculus	Austria	N	hemap	a
	Germany	N	hemap	a, k
	Switzerland	N	hemap	i
Falco cherrug	Romania	B	hemap	a
Falco mexicanus	Utah	B	h/occ	c
Falco sparverius	Colorado	B	hemap	i
	Maryland	B	hemap	i
	New York	B	hemap	i
	Utah	B	h/occ	c, d
	Mexico	N	sp. B	i
Falco sp.	Italy	B	hemap	a
COLUMBIDAE:				
Columba livia	Finland	N	hemap	a
Columba oenas	Finland	N	hemap	a
	Germany	B	hemap	k
TYTONIDAE:				
Tyto alba	Germany	N, B	hemap	a, k
	New Jersey	B	hemap	j
	Utah	B	occid	i
STRIGIDAE:				
Otus asio	Florida	N/B	flori?	a
	Arizona	B	occid?	e
Bubo ketupu	Malaya	B	orient	f
Aegolius acadicus	Brit. Columbia	B	hemap	i
"owl"	Mexico	B	sp. A	i

ntinued

	Nest (N)/ Bird (B)	Carnus Species	Ref.
	B	h/occ	d
	B, N	hemap	i
	N	h/occ	g
	B	flori	i
	B	hemap	a
	B	hemap	a
	N	hemap	a
	N	hemap	a
	N	hemap	a
	N	hemap	a
	N	hemap	a
	N	hemap	a
	N	hemap	a
	B	hemap	k
	N	hemap	a
	N	hemap	a
	N	hemap	a
ly,			
	N/B	hemap	a, i, k
	B	hemap	g, i
	N/B	hemap?	d
	N	hemap	a
	B	hemap	a, d, i
	N	hemap	a